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STUDIES ON THE HANDEDNESS OF THE FIDDLER CRAB, *UCA LACTEA*[1]

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The most characteristic feature of the fiddler crab is that the adult male has an enormously developed giant cheliped, while the other remains small; but the female has two small equal-sized chelipeds. The giant cheliped is not present in the early stages of males, but it develops enormously during the period of sexual maturation, and this has been studied by a number of authors. Yerkes (1901) collected numerous male specimens of *Uca pugilator* and *U. pugnax* at random and found that the numbers of right-handed and left-handed individuals were nearly equal. On the basis of this observation, he suggested that the handedness of fiddler crabs is determined primarily by chance. Later, Morgan (1923, 1924), experimenting with some young, sexually immature fiddler crabs, not only concluded that handedness is not determined in the early stages but also claimed that the accidental loss of one cheliped is the sole factor determining handedness. He reported that the giant cheliped always develops on the side of the remaining cheliped. On the other hand, Vernberg and Costlow (1966) claimed after a series of experiments that the handedness is determined genetically. The present author (Yamaguchi, 1973) examined about 5,000 adult males of *U. lactea* and found almost equal numbers of right-handed and left-handed individuals. Gibbs (1974) studied the handedness of male *U. burgersi* and found no significant difference between the numbers of left-handed and right-handed specimens.

In the present paper, observations and experiments designed to elucidate the factors involved in the determination of handedness in male fiddler crabs are presented.

Materials and Methods

Adult specimens of the fiddler crab, *Uca lactea* (de Haan), were collected from 1969 to 1975 from several habitats extending from Amakusa, Kyushu to Ishigaki-Jima, in the Ryukyu Islands (Table I). All the younger crabs and megalopae concerned in this study were collected from 1971 to 1975 from the tidal flats in the vicinity of the Aitsu Marine Biological Station in Amakusa. Megalopae were collected after they settled on the tidal flats, and the young crabs were collected by digging them out of their burrows.

All the megalopae and some of the young crabs were reared in 12 and 20 liter plastic aquariums. Pieces of gravel with a diameter of 3 to 5 cm were placed on the bottom of each aquarium. Over the gravel layer was put a layer of coarse sand

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and over it was placed sandy mud brought from the habitat of the young crabs. A part of the aquarium was left empty and sea water was exchanged through this space. The aquarium was filled with sea water at night, and it was pumped out in the daytime. The crabs were fed powdered dry fish and Wakamoto (a food supplement consisting of vitamins, amino acids, minerals, and proteins) in a ratio of one to three by volume. *U. lactea* is strictly diurnal, and it becomes inactive when it is dark, so each aquarium was illuminated with an incandescent bulb on cloudy days when the laboratory was dark. Two to 36 crabs of approximately the same size were reared together in each aquarium from 1971 to 1975. Most of the crabs were reared until it was clear whether the giant cheliped would be differentiated, usually a period of one to three months. However, some of the crabs were reared until they were sexually mature.

Results

Handedness of adult males

The results of examination of a total of 8088 adult males which were collected from eight local populations are summarized and presented in Table 1. Of these 8088, 4071 were right-handed (*i.e.*, the right cheliped was the giant) and the remainder were left-handed. No significant difference from a ratio of 1 : 1 in the

Table 1

Handedness of adult male U. lactea *having a carapace width greater than 7.0 mm. In Amakusa and Amami-O-Shima, the collection was carried out at three and two different sites, respectively.*

Locality	Year	Right-handed	Left-handed
KYUSHU			
Amakusa, site a	1969	312	315
	1970	902	877
	1971	791	801
	1972	113	117
	1973	482	464
	1974	533	525
	1975	273	273
Amakusa, site b	1970	86	96
Amakusa, site c	1970	51	52
Nichinan	1970	14	17
	1974	26	22
THE RYUKYU ISLANDS			
Amami-O-Shima, site a	1970	69	69
	1973	50	41
Amami-O-Shima, site b	1973	72	71
Okinawa-Jima	1972	30	21
Ishigaki-Jima	1972	169	161
	1973	98	95
Total		4071	4017

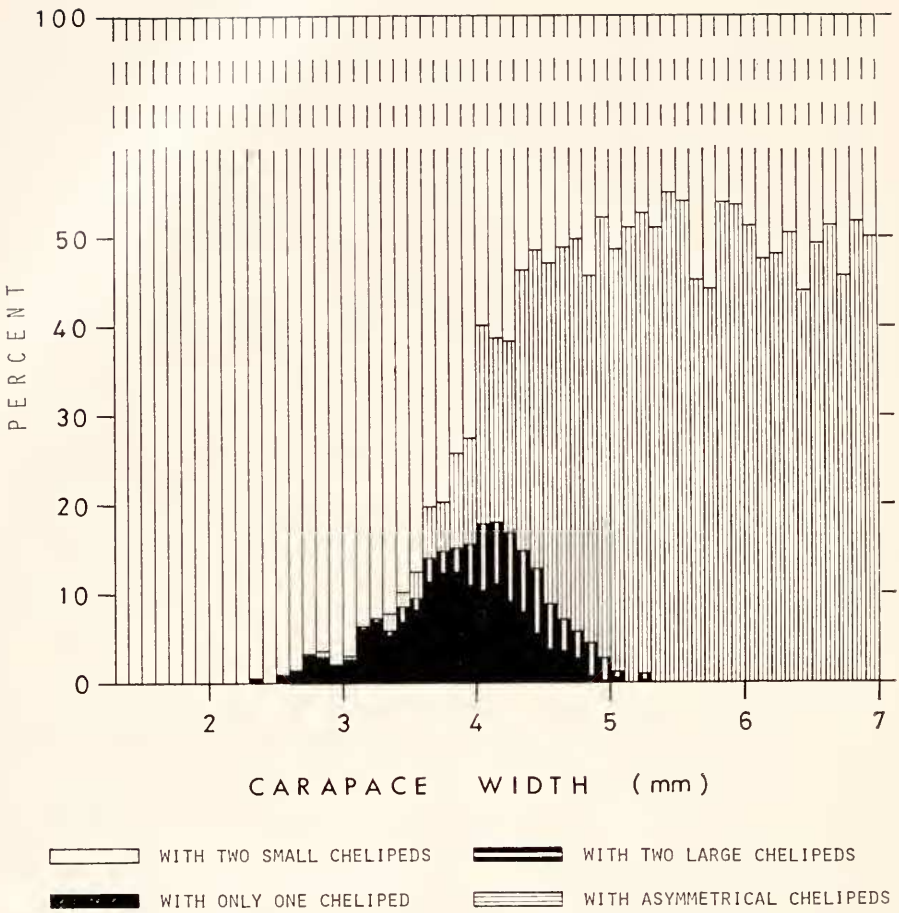

FIGURE 1. Percentage composition of the four kinds of cheliped-types in young crabs of *U. lactea*.

handedness of any of the studied populations was apparent. Furthermore, no significant annual fluctuation in handedness was observed. No adult male having either two giant chelipeds or two small chelipeds was collected.

Chelipeds of young crabs

A total of 13,913 young crabs with a carapace width (CW) less than 7.0 mm was examined. The results are summarized in Figure 1. These data indicate that growth and differentiation of the giant cheliped in males begins in crabs with a carapace width of around 2.5 to 5.0 mm. Almost all the crabs smaller than 2.5 mm still have undifferentiated chelipeds, with both chelipeds being small. Among the transitional crabs, those between the undifferentiated and differentiated stages, those with a carapace width of 2.3 to 5.2 mm, some with only one cheliped and

others with two large chelipeds were noticed. Indeed, over 10% of the crabs with a carapace width of around 4 mm had one of these two types of cheliped arrangements. The total number of young crabs lacking their right cheliped was 318, while 293 had lost their left cheliped. The total number of the young crabs with two large chelipeds was 300. The large chelipeds of young males differ in size relative to the carapace width of the giant cheliped from adult males, the small chelipeds of those young males that still have them, and those of adult females. In short, the large chelipeds of the young crabs are intermediate between the small and giant ones.

The numbers of the two sexes were nearly equal after differentiation of the chelipeds had occurred. The sex was determined by examining the abdominal

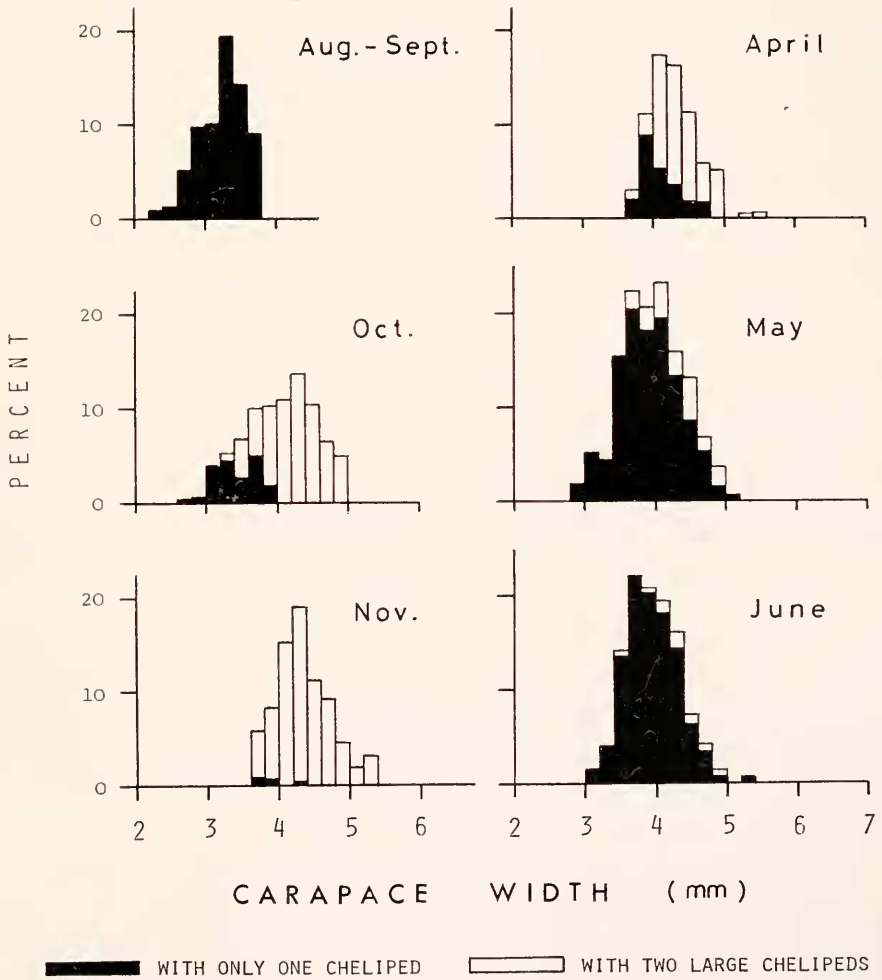

FIGURE 2. Monthly variation of the percentage of young crabs with only one cheliped or with two large chelipeds.

appendage or outer appearance of the abdomen. Both male and female pleopods began to develop at about 3 mm CW, but it was impossible to always distinguish the sexes externally until the crabs became larger than 5 mm CW, for the abdomen of a small-sized female is similar in form and size to that of a young male.

There was a distinct seasonal variation in the percentage of young crabs having only one cheliped or two large chelipeds. In Figure 2, their monthly percentage frequencies are shown. In September and early October young crabs with only one cheliped occurred in high frequency, but those with two large chelipeds were absent or present in only low frequency. The frequency of the former dropped greatly after the middle of October, while that of the latter rapidly increased. In November, of 1307 crabs collected three had only one cheliped, while there were 73 with two large chelipeds.

Young crabs feed and move about actively in September and October, but their activity decreases gradually as the temperature drops in early November, and all the crabs disappear from the surface and hibernate in their burrows during the winter season, from early December to early March. Some of the young crabs begin to appear on the surface about the middle of March, and all have emerged by the end of April. Young crabs with two large chelipeds are still present in high percentage through the middle of April, but the percentage decreases by the end of April. On the other hand, young crabs with only one cheliped increase greatly in number during early May. Most of them had the large cheliped as the remaining one.

Rearing of young crabs with only one cheliped

Eighty-six young crabs having only one cheliped with a 2.3 to 4.4 mm CW (37 were without their right cheliped and 49 without the left one) were brought to the laboratory and reared for 46 days and yielded 53 surviving crabs at the end of rearing. All the survivors were male and attained a CW of 3.8 to 6.2 mm; of these, 26 were left-handed and 27 right-handed. In all cases, the giant cheliped developed on the side that had a cheliped when the crabs were collected, and only a small cheliped formed on the side where one had originally been lost.

Rearing of young crabs with two large chelipeds

In one experiment of this set, 23 crabs with a 4.1 to 5.3 mm CW were reared from the middle of April to the end of May, and all of them survived. They were all males and each discarded one of its chelipeds and the cheliped asymmetry differentiated during this period. Twelve became right-handed males and 11, left-handed ones.

In another experiment, 55 young crabs (3.6 to 4.7 mm CW) were reared from the end of November to July of the following year. Thirty-eight crabs survived. One cheliped was discharded by 35 of these crabs and asymmetry developed. Nineteen males were right-handed and 16 left-handed. The remaining three crabs did not lose a cheliped, and both chelipeds grew equally, each of the three crabs finally developing two giant chelipeds. The sizes of these three males ranged from 9.5 to 10.0 mm CW at the end of rearing. One of them lost its right

cheliped as a result of a fight when the crab was about 6 mm CW but regenerated the giant cheliped again and retained the two giant cheliped condition.

The results of rearing show that young crabs with only one cheliped always develop the giant cheliped on the side of the remaining cheliped and the small one forms on the side of lost cheliped. Even in those young crabs that first form two large chelipeds, one of them normally is discarded with the ultimate appearance of cheliped asymmetry in the adult male. Thus, discarding or losing one cheliped seems likely to be the normal process whereby the one-handed character of this species is attained. The three crabs reared in the laboratory that developed and retained two giant chelipeds were exceptional, because no such male was encountered in any of the natural habitats.

Removal of the large cheliped from young males with asymmetrical chelipeds

In order to learn whether cheliped asymmetry could be reversed in this species, the large cheliped was removed from the small-sized males. The young males were easily induced to discard a cheliped by autotomy when it was squeezed by a pair of forceps and pulled lightly. One hundred and fifty-nine males were used; 80 were left-handed and 79 right-handed. They were reared for 58 days after the operation. The body size of the crabs at the beginning of the experiment ranged from 3.2 to 4.1 mm CW, and they grew to 4.8 to 6.8 mm CW by the end of the experiment. One hundred and twenty-six males survived and 124 males retained the same handedness they had before the operation. Two regenerated the small cheliped instead of the giant one and had a female-like appearance.

Another set of experiments was then carried out in which both chelipeds, large and small, were removed simultaneously from young males. One hundred thirteen individuals (50 right-handed and 63 left-handed) were used. Their sizes ranged from 3.4 to 4.5 mm CW. They were kept until the chelipeds regenerated (70–80 days). One hundred and six crabs with a size range of 4.2 to 9.2 mm CW survived. The handedness of the surviving males was exactly the same as before the operation. These results clearly show that the handedness of male crabs is firmly established after the appearance of the asymmetry.

Removal of one cheliped from megalopae and from young crabs that still have two small chelipeds

The right cheliped was removed from 246 megalopae, and they were reared for 73 days, and grew to be crabs of 4.4 to 7.3 mm CW. Forty-four females and 33 males survived until the end of this experiment. All the males developed into left-handed individuals.

The right cheliped was likewise removed from 692 first stage crabs. They were very small in size, 1.3 to 1.5 mm CW, at the time of the operation and were reared for 55 to 65 days by which time they had attained a 5.0 to 6.4 mm CW. The survivors consisted of 193 males and 206 females. The surviving males were all left-handed. The same experiment was performed a second time with 770 slightly larger crabs (1.8 to 4.5 mm CW) that were reared for 55 to 135 days and grew to 3.5 to 7.0 mm CW. Three hundred and eighty-five females and 165 males survived. Of the 165 males, 163 were left-handed, one of the remaining

two was right-handed and the second had female-type chelipeds. This female-type male had normally developed male pleopods and his size was 5.8 mm CW. These results are summarized in Table II, according to the sizes of the individuals at the time of operation. There was a large difference between the numbers of surviving males and females when the larger-sized individuals were operated upon, resulting mainly from the difference between the numbers of both sexes at the time of the operation. The percentage of males keeping the two small cheliped condition decreased with the increase in size (Fig. 1), and at approximately 4.5 mm CW, almost all the individuals with two small chelipeds were female.

An experiment in which the left cheliped was removed from 23 young crabs (size 3.3 to 3.5 mm CW) that had two small chelipeds was also performed. Eight females and three right-handed males survived after 246 days.

The results of these experiments indicate that the loss of one cheliped from megalopae and young crabs which still have not exhibited cheliped asymmetry is absolutely essential for the differentiation of handedness in males. The crabs used in this experiment that had two small chelipeds showed no sign of handedness in either sex. Removal of one cheliped resulted in the development of a large cheliped on the other side in almost every instance. This seems to support the assumption that the handedness of this species is not determined in the early stages of growth, but is determined only when a cheliped on one side is lost or removed.

Removal of both chelipeds from megalopae and young crabs with symmetrical chelipeds

Two chelipeds were removed from 35 young crabs, 3.6 to 4.8 mm CW in which two large chelipeds had developed. The crabs were reared for 44 days after the operation and grew to 6.0 to 8.1 mm CW. Twenty-one males survived, but none had a giant cheliped; all chelipeds were small like those of a female.

Both chelipeds were likewise removed from megalopae and young crabs which still had two small chelipeds. A total of 269 megalopae were subjected to the operation and were reared for 296 days, becoming young crabs of 5.6 to 10.3 mm CW. Fourteen females and 15 males survived. Of the males, 13 did not develop a giant cheliped, but possessed only two small chelipeds. It was difficult to rear such young individuals after the operation. Most of them died before metamorphosis. A total of 1098 crabs were also subjected to the operation. Among them, 317 were first stage crabs with a 1.4 to 1.5 mm CW at the time of operation and were reared for 308 to 317 days. Fifty-three females and 47 males with a 4.8 to 8.9 mm CW survived. Forty-two of the 47 males developed only two small chelipeds. An additional 781 crabs had a CW of 2.5 to 4.2 mm, 333 females and 120 males of these having survived until the end of rearing. Of the surviving males, 110 did not develop a giant cheliped. About one-half of the males were reared for 75 days after the operation, but the rearing of other half was continued for 295 to 726 days to observe whether their cheliped condition would change; males with a 6.9 to 13.1 mm CW were finally obtained. No change of the cheliped condition was observed. Most of the males kept two small chelipeds. The results were arranged according to the sizes at the time of the operation and are presented in Table III. One hundred and fifty-two of the

TABLE II

Differentiation of the giant cheliped of U. lactea *after removal of the right cheliped from megalopae and young crabs with two small chelipeds.*

Size at time of operation (CW, mm)	Number of operated crabs	Female	Surviving males		
			Left-handed	Right-handed	With two small chelipeds
Megalopa	246	44	33		
1.3–1.5	692	206	193		
1.8–1.9	103	28	25		
2.2–2.3	42	10	9		
2.4–2.5	59	28	21		
2.6–2.7	65	34	24		
2.8–2.9	32	13	12		
3.0–3.1	34	13	7		
3.2–3.3	24	13	8		
3.4–3.5	31	5	3		
3.6–3.7	94	50	22		
3.8–3.9	92	47	14		
4.0–4.1	100	73	10	1	
4.2–4.3	73	54	7		1
4.4–4.5	21	17	1		
Total	1708	635	389	1	1

167 males obtained in this experiment did not develop the giant cheliped, which seems to be the most characteristic feature of the male fiddler crab, but instead kept two small chelipeds as in female crabs. It was hard to distinguish these males from true females without examining their abdomens. Some of these males which had become sexually mature were bred to mature females in order to determine whether their reproductive system functioned normally. The females laid eggs

TABLE III

Differentiation of the giant cheliped after the removal of two chelipeds from megalopae and young crabs with two small chelipeds.

Size at time of operation (CW, mm)	Number of operated crabs	Female	Surviving males			
			With two small chelipeds	With two large chelipeds	Left-handed	Right-handed
Megalopa	269	14	13	1	1	
1.4–1.5	317	53	42	3	2	
2.5–2.7	216	51	44	3	1	2
2.8–3.0	13	1	1			
3.1–3.3	138	35	23			
3.4–3.6	91	39	8			
3.7–3.9	130	87	14			3
4.0–4.2	193	120	20		1	
Total	1367	400	165	7	5	5

which underwent normal development and hatched. It appears that the males with two small chelipeds obtained from this experiment do have a normal reproductive ability. However, they obviously could not entice females to their burrows by a waving display with the giant cheliped as do normal males (Yamaguchi, 1971). They copulated instead at the entrance of the female burrows. These experiments showed that the simultaneous loss of both chelipeds before the differentiation of asymmetry prevents the development of a giant cheliped.

Removal of one cheliped from the males that regenerated two small chelipeds

To determine the effect of repeated extirpation of one cheliped on the subsequent differentiation of the chelipeds, both chelipeds were first removed from 392 young crabs of a size of 2.7 to 4.3 mm CW. Fifteen to 51 days after the initial operation, all the survivors had regenerated two small chelipeds. The crabs had grown to 2.8 to 7.2 mm CW at the time. Only the right cheliped was then removed again and the crabs were reared for 55 to 70 days following the second operation. One hundred males with a CW of 6.0 to 9.2 mm were obtained. Of these, 94 had two small chelipeds, one was right-handed, three were left-handed, and two had two large chelipeds. Compared to the former experiment, no significant increase of males with a left-handed giant cheliped was obtained. Most of the males with a left-handed giant cheliped was obtained. Most of the males kept two small chelipeds. These results indicate that once the young crabs have suffered simultaneous loss of both chelipeds, the two small cheliped state becomes established, and this condition is not easily changed.

Effect of time interval on removal of two small chelipeds from young crabs

In this series of experiments, both chelipeds were removed from young crabs with two small chelipeds, but instead of the removal being carried out simultaneously, there were various time intervals between the removal of the right cheliped and the subsequent removal of the left cheliped. Seven hundred and forty-seven

TABLE IV

Results of removal of the right cheliped from young crabs, followed by removal of the left one 12 to 192 hours later.

Interval (hr)	Number of operated crabs	Surviving males		
		With two small chelipeds	Left-handed	Right-handed
12	20	6		
24	130	28	5	
48	123	23	10	
72	99	24	10	1
96	241	25	12	2
144	52	4	17	
192	82	1	28	
Total	747	111	82	3

young crabs of the size 2.0 to 3.9 mm CW were used. At the first operation, the right cheliped was removed, and at the second operation, the left cheliped was extirpated. The time intervals between the two operations were 12, 24, 48, 72, 96, 144, and 192 hours. The crabs were examined 150 to 190 days after the second operation, and the resulting data are summarized in Table IV. Of the 747 crabs operated upon, 196 males survived until the end of the experiment. One hundred eleven of these 196 had two small chelipeds, 82 were left-handed, and 3 were right-handed. The left-handed males obtained from these experiments were few in number, about one-third, when the time interval between the first and the second operations was less than 96 hours; but when there was a longer time lapse, the ratio of left-handedness increased dramatically, 17 out of 21 males became left-handed in the 144 hour set and 28 out of 29 in the 192 hour set. It appears that handedness in males of this species is not determined immediately after the artificial loss of both chelipeds from young crabs unless there is a certain length of time between the loss of the two chelipeds. From this experiment, it appears more than 96 hours may be necessary. When the cheliped was removed before this point, a large number of male crabs with two small chelipeds were produced, whereas after this point, most male crabs developed distinct handedness.

Discussion

As has been reported by Morgan (1923, 1924), there are four types of cheliped arrangement in young fiddler crabs, *i.e.*, with two small chelipeds, with two large chelipeds, with one small and one large cheliped, and with one cheliped lost. The appearance of young crabs with two large chelipeds is noted. The results of rearing experiments showed that they are all males and lose one of their chelipeds later in life and thus attain cheliped asymmetry. However, no functional handed-character or morphological difference could be distinguished between the chelipeds before one was lost. A few reared crabs did not lose a cheliped and grew to be adult males with two giant chelipeds. The existence of the stage with two large chelipeds and the appearance of adult males having two giant chelipeds, though no such individual has been collected in its natural habitat, suggest that the chelipeds of young males have an equal potential for growing into the giant in adult males. Based on the results of observations and experiments, the general or fundamental pattern of growth of the asymmetrical chelipeds in male crabs of *Uca lactea* is the following. First, each cheliped has an equal potential to grow and differentiate into a giant cheliped during the early growth period. Secondly, if one cheliped is lost or damaged, the regenerating cheliped loses its potential to differentiate into a giant cheliped. Under natural conditions, the young male loses one of his chelipeds when he reaches a CW of 2.3 to 5.2 mm. The remaining cheliped grows into a giant and cheliped asymmetry is accomplished. Thirdly, if both chelipeds are extirpated simultaneously, both lose the potential, and the crab is unable to ever form a giant cheliped.

The cause of loss of one cheliped at the limited stages of growth is not clear. However, the loss has some relation to the environmental conditions, especially temperature. The frequency of young crabs with only one cheliped was high in October and May (Fig. 2) and the temperature of these months in Amakusa was

19.3° C and 19.0° C, respectively. During the period from November to April, the frequency of young crabs with two large chelipeds increased greatly, and the average temperature during this period was 10.3° C. The seasonal variation of cheliped condition in young crabs can be explained as follows: in the warmer season, young males normally lose one of the chelipeds when they are small in size; while under lower temperatures, the loss of a cheliped may not occur so regularly and growth of the crab is more even, so that some young males grow to the size at which large chelipeds are formed becoming the ones with two large chelipeds. Such males keep their two large cheliped condition temporarily under low temperature, and only lose one of their chelipeds later when it becomes warmer, thus changing into males with only one cheliped. As mentioned above, a few crabs developed and retained two giant chelipeds in the laboratory. However, no such individual was found in 8088 adult males collected in the natural habitat (Table I). It seems certain that the artificial condition in the laboratory prevented the loss of one of the chelipeds; however, the relation between the environmental factors and the process of cheliped loss is not clear at the present. During the warmer seasons the crabs are more active, and the chance of fighting is supposed to increase; however, fighting does not seem to be the usual cause of cheliped loss. A considerable number of young crabs with only one cheliped were found in habitats with a very low population density (below $5/m^2$) and also in ones with very high densities (above $100/m^2$). Young crabs with a CW of 2 to 5 mm feed within a radius of 10 cm from their burrows and rarely stray from this area; therefore, the probability of an encounter and struggle with another individual is very low when the density is lower than $10/m^2$. If fighting is the cause of cheliped loss, there should be some males which have no chance to fight, becoming adult males with two giant chelipeds. No such male was found in any natural habitat. It is highly probable that most young males lose one cheliped spontaneously.

It is clear that the giant chelipeds of adult male fiddler crabs begin to differentiate at a definite period in their life cycle, with a CW of around 2.5 to 5.0 mm. As is well known, the secondary characteristics of many Crustacea are under the control of the androgenic gland (Adiyodi and Adiyodi, 1970; Charniaux-Cotton, 1962; King, 1964). It seems probable that, in the present species also, differentiation of the giant cheliped of males is under the control of the androgenic hormone. Although the development of the androgenic gland in the present species has not been studied, it is highly possible that the cheliped in the male changes in its response as a target organ of the hormone produced from the androgenic gland after its removal or extirpation. If this assumption is reasonable, the competence of the chelipeds for the male hormone might be lost for a short period after the cheliped is damaged or removed.

It has long been known that, when the removal of either one of the chelipeds or both of them is carried out on adult males, no change in handedness occurs when the chelipeds regenerate (Prizibram, 1917). The handedness of adult males, therefore, becomes firmly established once it has appeared. In the present experiments, the removal of the giant cheliped or both of the chelipeds was carried out on younger males, some of which had not experienced molting after the establishment of asymmetry. The result was the same as in the case of adult males, and almost all of the younger males reestablished the same handedness. In this

connection, the results of experiments in which the effect of a time interval on removal of two chelipeds offer the interesting notion that the establishment of handedness requires a certain time interval after the loss of one cheliped; in the experiment it was about 96 hours. Ninety-six hours after one cheliped is removed or lost, handedness becomes established firmly, and it cannot be changed by the successive removal of the remaining cheliped. By the successive removal of one cheliped from the males which regenerated two small chelipeds, it became clear that the two small cheliped condition was firmly established in them. The male which developed two giant chelipeds did not change its exceptional cheliped condition after the loss of one of its giant chelipeds. These facts show that once the definitive cheliped condition has been established, further loss or removal of either cheliped is not enough to change the cheliped condition.

The results of the population studies on the handedness of the present species seem to support strongly the conclusion of Yerkes (1901) that the handedness of fiddler crabs is determined by chance. However, as has been reported in a previous paper (Takeda and Yamaguchi, 1973), the natural population of *Uca marionis* showed that almost all of the adult males were right-handed; of the 567 specimens collected, 554 were right-handed and only 13 left-handed. It seems reasonable to consider that the handedness of *U. marionis* is controlled not accidentally but genetically. However, it was possible to induce most of the males to have left-handedness by the removal of the right cheliped when they were in the two small cheliped stage. The mechanism of normal determination of handedness in this species is not clear, but it seems certain that the adult handedness in *U. marionis* also can be predetermined by which one of the small chelipeds is removed in the immature stages (Yamaguchi, unpublished). Vernberg and Costlow (1966) extirpated one cheliped from larger-sized young crabs of *U. rapax* and *U. pugilator* with symmetrical chelipeds. Among the surviving 19 males, five developed a giant cheliped in place of the cheliped removed. Based on this result, they concluded that the handedness of the fidddler crab is determined genetically. It is not clear at present whether the cause of the difference between their results and those of this study depends on the species difference or on a size difference.

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Summary

1. The numbers of right-handed and left-handed males of *Uca lactea* were nearly equal, and no significant regional or yearly differences from the ratio of 1 : 1 were found.

2. In the early stages of growth, all the crabs had two small chelipeds, and no morphological differences were found between the sexes. All males with a carapace width greater than 5.3 mm exhibited cheliped asymmetry. Apparently,

a male normally loses one of his chelipeds which then regenerates into a small cheliped; the remaining cheliped develops into a giant, and the male attains his cheliped asymmetry.

3. Artificial removal of one cheliped from megalopae and young crabs whose chelipeds were still in the symmetrical condition induced handedness. The large cheliped always developed on the intact side.

4. When males suffered the simultaneous removal of both chelipeds in their megalopa or crab stage before the attainment of asymmetry, they could not develop a giant cheliped but instead kept two small chelipeds permanently. However, no abnormality was recognized in their reproductive function. If a male did not lose a cheliped, two giant chelipeds developed.

5. Once the handedness was established in a male, it could not be reversed by the subsequent removal of one or both chelipeds.

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